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A New Ethospecies of Stenogaster Wasps from Sarawak,
with a Comment on the Value of Ethological
Characters in Animal Taxonomy*,**

With 6 Text-figures

Shôichi F. SAKAGAMI and Kimio YOSHIKAWA

*Zoological Institute, Hokkaido University, Sapporo and Laboratory
of Animal Physiology, Osaka City University, Osaka
(Communicated by T. UCHIDA)*

ABSTRACT A new species of stenogasterine wasp, *Stenogaster calyptodoma*, is described from Sarawak. The species is distinguished from *S. micans* mainly by the nest architecture. A comment is given as to the value of ethological characters in taxonomy. The ethological characters are apparently auxillary from the practical point of view, but there is no theoretical basis to support their categorical inferiority as diagnostic characters.

On our visit to Sarawak in September, 1966, as members of the Osaka City University 5th Scientific Expedition to Southeast Asia, we discovered a singular nest of a stenogaster wasp. The single female obtained from the nest was closely similar to *Stenogaster micans* (Saussure, 1852), differing only in a few superficial characters, mainly in yellow color marks. On the other hand, the nest architecture showed a remarkable departure which is considered to be a valid basis for erecting a new species separate from that of *S. micans*.

Stenogaster calyptodoma sp. nov.

Female: Closely similar to *S. micans* (Fig. 1), except for the following features: 1) Punctuation on frons less uniform, with admixture of both coarse and minute spots (Fig. 2, A~B). 2) Supra-antennal mark large and rounded (Fig. 2, A~B). 3) Gena below with yellow patch along outer orbit. 4) Lateral pronotal mark absent (Fig. 2, C~D). 5) Basal band on metasomal tergum II fused (Fig. 2, Q to R and S).

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** A joint contribution from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo (S.F.S., No. 798) and the Laboratory of Animal Physiology, Faculty of Science, Osaka City University, Osaka (K.Y., No. 83).

Nest: Outer envelope completely separated from brood cells, not made as extension of outer walls of peripheral cells (Fig. 6, A and B to C). Apical keels on envelope forming continuous and distinct ridges, not made from rows of denticles (Figs. 6, F to D and E), and reaching apex of funnel-like widened entrance tube.

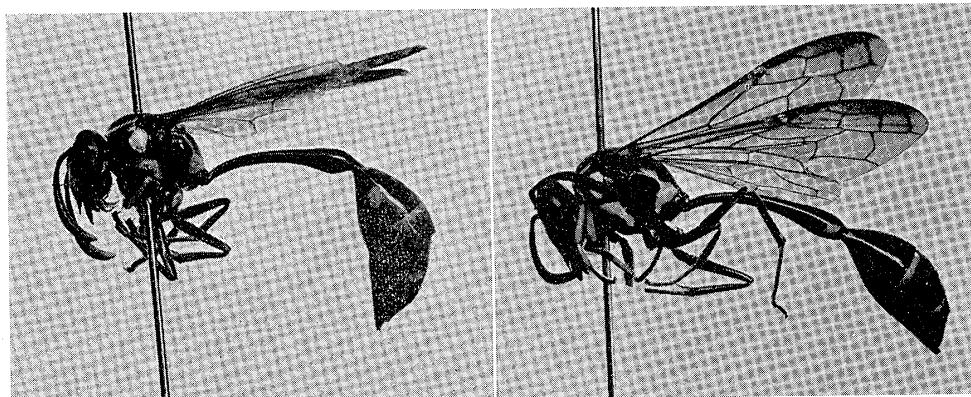


Fig. 1. Females of *Stenogaster calyptodoma* sp. nov. (left) and *S. micans* (right), the latter specimen is from Bokor, Cambodia.

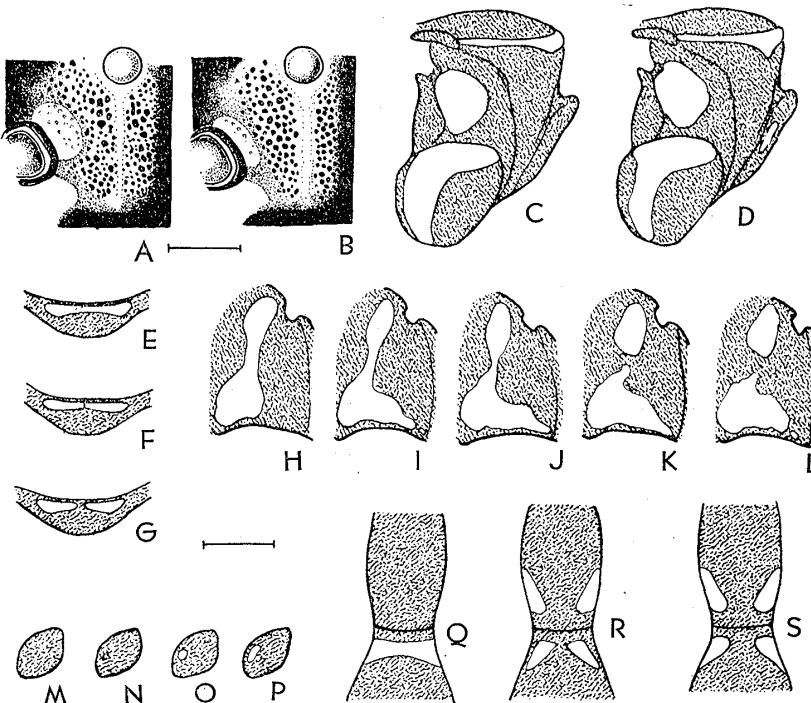


Fig. 2. Differences in punctuation (A~B) and yellow marks between *S. calyptodoma* sp. nov. (A, C, E, H, M, Q) and *S. micans* (B, D, F~G, I~L, N~P, R~S). A~B. Punctuation on frons, together with suprarentinal mark; C~D. Yellow marks on mesosomal sides; E~G. Metanotal mark; H~L. Propodeal mark; M~P. Tegular mark; Q~S. Marks on metasomal terga I and II. (Scale=0.5 mm in A~B, 1 mm in the other figures).

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Holotype: 1♀ (Body length 16.5 mm, Length of fore wing 12 mm) with nest, Kampong Astana near Kuching, Sarawak, Malaysian Borneo, IX 8, 1966, deposited in the Zoological Institute, Hokkaido University.

Besides the characters mentioned above, the specimen differs from those of *S. micans*, mainly taken in Thailand and Cambodia, in the following yellow marks: 1) Lower mesopleural mark not narrowed below (Fig. 2, C to D). 2) Propodeal mark not enlarged below (Fig. 2, H to I~L). 3) Metanotal marks fused together (Fig. 2, E to F~G). 4) Tegular mark absent (Fig. 2, M to N~P). These features were excluded from the diagnosis, considering their possible variation, although the difference in the shape of the propodeal mark seems to be relatively stable, in comparison with that of other species. However, even some of the characters included in the diagnosis might become invalid, if a closer variation study were to be carried out. Any conscientious taxonomist would undoubtedly hesitate to regard the present case as more than a mere color variant of *micans*, unless the specimen was accompanied by the nest.

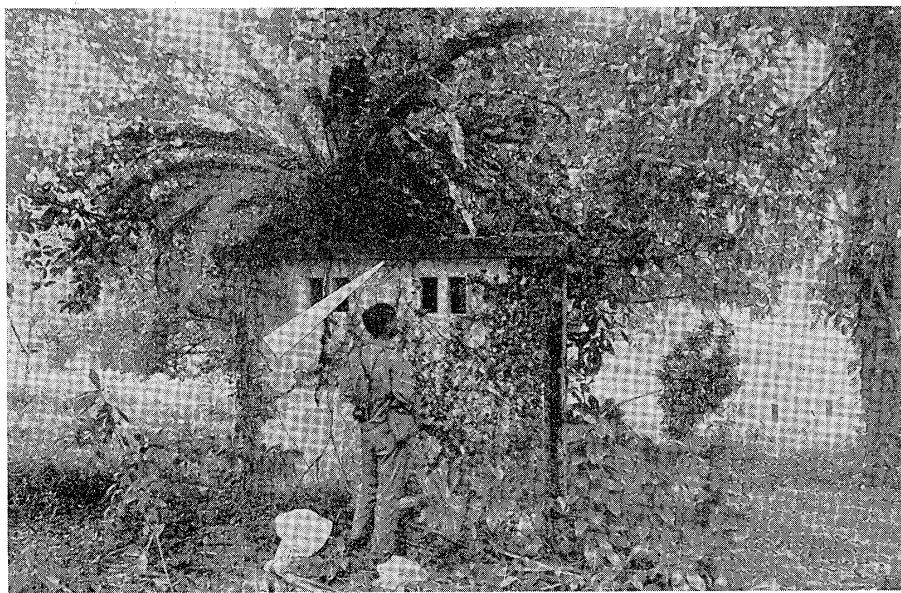


Fig. 3. Nesting site of *S. calyptodoma* sp. nov. indicated by arrow.

The nest was found under the overhang of the eaves of a ruined concrete construction. The substrate surface was horizontal and flat, about 2 m above the ground (Fig. 3). A small comb of about 15 mm in diameter, consisting of seven cells, was directly fixed to the substrate surface. The nest envelope was also fixed to the substrate surface, completely covering the comb but distinctly separated from the latter by a distance of ca. 5 mm (Fig. 4, Left and Right). The envelope resembles the upper half of a sand hourglass, widest at the base, with a diameter of 26 mm, gradually narrowing to the entrance tube, with a minimum diameter of 6 mm. The apical part is slightly enlarged to 8 mm in diameter. Total length is ca. 42 mm and the length of the entrance tube, ca. 11 mm.

The outside of the envelope is provided with 10 keels, each forming a

distinct continuous ridge, running without interruption from the base to the apex of the envelope, with a single exception, which ended at 6 mm from the base. Keels are arranged more or less equidistantly (distances are, 9, 8, 5, 16, 6, 11, 17, 4 and 9 mm at the base of the envelope). The interkeel walls show angular transverse stripes, suggesting the building manner, advancing along the keels while delaying at the intermediate spaces. Similar angular stripes are also seen in the nests of *S. micans* and related species. At the apical portion of the entrance tube, the spaces between the keels become very narrow, and are provided with many pores, resulting in a lacework architecture. The keels project a little beyond the interkeel walls.

Completed cells are 14 mm in length, about 5 mm in basal diameter, slightly swollen in the middle (6 mm). Cell walls show transverse but not angular stripes. The individual cells were as follows: Nos. 1, 2, 6, half-built and empty;

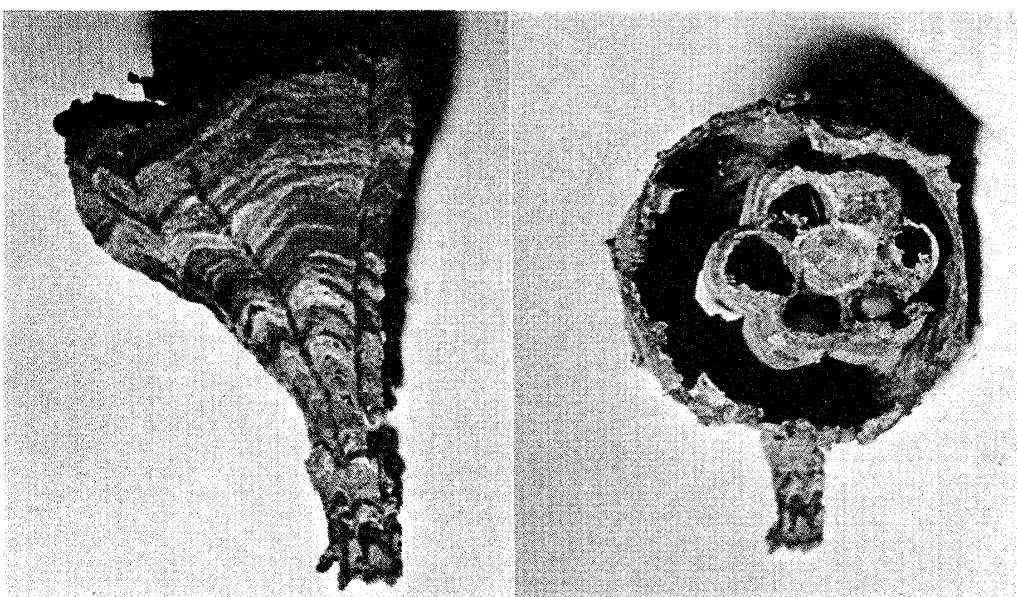


Fig. 4. Nest of *S. calyptodoma* sp. nov. Left. Lateral view. Right. Seen from above after removed from the nesting substrate.

Nos. 3, 4, 5, 7, fully built with pupae (*cf.* Fig. 6, A). In cells containing pupae, the base of the cell was covered by a spun fibrous film, but the pupa was exposed, not covered with a proper cocoon, which is an unusual trait of the Vespidae (*cf.* Williams, p. 169). Another more singular characteristic is that the entrances of these cells are constricted to 4 mm but invariably open. Therefore, the pupae are directly exposed to the outer world, a trait very rarely found in Aculeata. The position of the pupae in the cells is as given by Williams: "The pupa is so bent upon itself that the mandibles touch the end of the body, and it is the head and upper thorax side of the triangle which form a base a little wider than the cell's mouth."

Two alternative interpretations are held concerning the developmental phase of the nest: 1) The female found in the nest is the original foundress, and restarted her brood-rearing activity by repairing the cells, after an inactive

phase (suggested by the absence of young immature stages). 2) The female is one of the first daughters of a previous foundress. She succeeded to the mother's nest and started her building activity. Although no definite answer can be given to these possibilities, the following facts favor the first assumption. First, the wings of the female captured are quite worn, indicating her relatively old age. Further, three cells, one containing the pupa and two short and empty ones, have a similar arrangement of transverse stripes (Fig. 6, B).

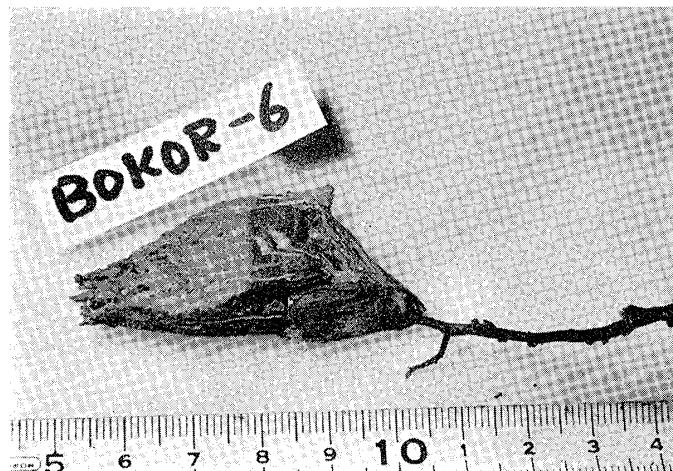


Fig. 5. Nest of *S. micans*, showing keels consisted of rows of denticles and fine longitudinal ridges.

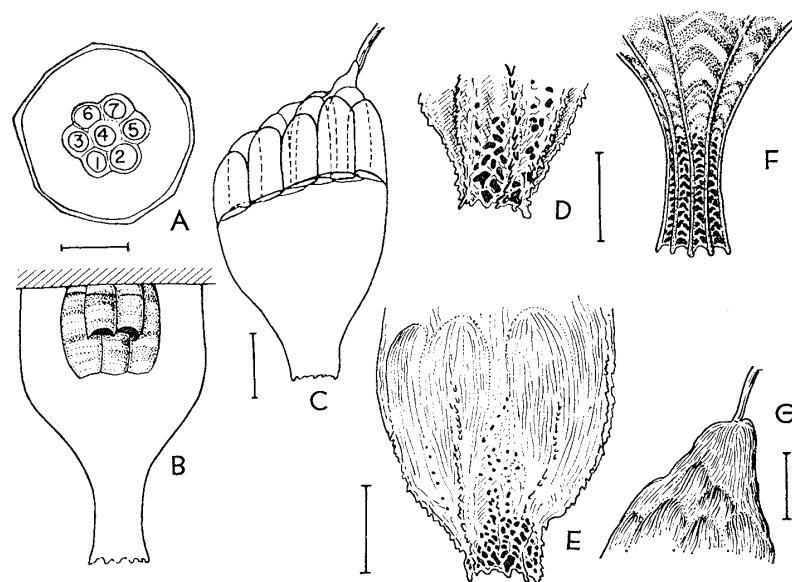


Fig. 6. Nests of *S. calyptodoma* sp. nov. (A, B, F) and *S. micans* (C, D, E, G). A. Arrangement of comb and envelope seen from above. B~C. Same, lateral views. D~F. Lower part of nest, showing surface architecture. G. Upper part of nest, showing fine longitudinal ridges (Scale=1 cm).

Probably this indicates the synchronous building of these three cells. Seemingly, the two empty ones were in the process of being repaired by the foundress, after the emergence and dispersal of the adults reared within them.

The most interesting aspect of the nest architecture is the structure of the envelope entirely separated from the comb. More than 30 nests of *S. micans* and related species, found during our expedition were invariably attached to twigs, rootlets, or similar structures, rather than to a flat substrate. Moreover, the envelope was always made by the extension of the outer walls of the peripheral cells. The previous descriptions and illustrations of this group seem to confirm our observation (Bingham, 1890; Williams, 1919; Schultheiss, 1927; Pagden, 1958; Iwata, 1967). The nest of *S. calyptodoma* represents the first discovery of a nest with a true envelope (=calyptodomous nest, cf. Saussure, 1853-58; Richards and Richards, 1951) in stenogasterine wasps.

An objection to our interpretation could be made by explaining the different envelope types as the result of behavioral plasticity, that is, by the possible appearance of a separate envelope caused by the selection of a flat and broad nesting substrate. We believe, however, that the validity of our interpretation is supported by the following reasons:

- 1) First, the nest site preference is relatively fixed among stenogasterine wasps. Certainly some species are relatively plastic in the preference of nesting ground, choosing thin rootlets or relatively thick ones, or fixing the nests to thick roots or broad substrates. But such difference as seen between *micans* and *calyptodoma* is very rare. Among hundreds of nests observed by us, we found no single instance of such wide plasticity within one and the same species.
- 2) Even if the present case represents a rare instance of such plasticity, there is no circumstantial obstacle to the building of a pseudovenvelope by the foundress, by extending the outer walls of the peripheral cells. Though not belonging to the *micans* group, *S. flavolineata* (Cameron) often builds nests of mud under overhanging rocks, that is, on the broad substrate. The outer walls of the peripheral cells are extended at one side of the nest, though not so widely as to be called an envelope.
- 3) A further objection would be possible by postulating an innate behavior mechanism, which is relatively plastic and allows the occasional construction of a separate envelope, the manifestation of which is, however, usually inhibited by the spatial limitation caused by the nesting substrate. Even if this assumption were valid, the difference in the surface microarchitecture of the envelope favors the specific distinction between *micans* and *calyptodoma* as given below.
- 4) As any nests are the outcome of the gradual elaboration by the builder, we must compare the nests at the final developmental phase in order to get some stable characteristics. Among more than 20 nests of *micans* observed by us, including a dozen apparently at the final phase, the keels were always formed by rows of denticles, not representing distinct ridges as in *calyptodoma*. Further, the keels are indistinct on the entrance tube, where it gradually narrows toward the tip, not enlarged as in *calyptodoma*. The lacework on the

entrance tube of *micans* is also less differentiated than in *calyptodoma*, often giving an impression of randomly scattered pores, which are not confined to the tube proper, but, though less densely, found also on the lower half of the main body (Fig. 6, D and E). Moreover, at the final architectural phase, the nest surface of *micans* is invariably provided with numerous delicate ridges running longitudinally, which are incomparably finer than the keels in *calyptodoma*, but usually made as continuous ridges, not as rows of denticles (Fig. 6, E and G). In the nest of *calyptodoma*, the outer surface of the envelope is, except for the main keels, homogeneously coarse, without such microridges, even when the nest is indubitably at the final architectural phase. Judging from the comparison of the nest architecture of various stenogasterine species, these differences are enough to be called specific, although there is no direct evidence of their genetic stability.

For these reasons, we regard *S. calyptodoma* as specifically distinct from *S. micans*, representing a further instance of the ethospecies proposed by Emerson (1956).* For the time being, the species is also distinguished from *S. micans* by some morphological features. But the ethological features mentioned above are sufficient to separate two species, even if the morphological distinction should be invalidated, by the inclusion of the characters given in the diagnosis within the variation range of *micans*. *S. calyptodoma* would become synonymous with *S. micans* only when an extreme ethological plasticity of the latter species would be confirmed; that is, when the two nest patterns were proven to be two different phenotypic expressions of a common genetic mechanism. At the present, we prefer to adopt the specific difference, first of all, in order to call attention to the remarkable ethological diversity in stenogasterine wasps. The proposition by Pagden (1958), followed by Iwata (1967), concerning the necessity of collecting specimens together with nests, must be stressed here again.

On this occasion, one of us (S.F.S.) would like to comment on the importance of ethological characteristics in taxonomy. Many taxonomists tend to regard the ethological characters as only auxillary to the morphological ones. This attitude is certainly recommended in practice. Many ethological characters are established only by observations on living individuals, often after long and tedious field work, which is impossible to do or nearly so in many "rare" species, mainly erected on the basis of morphological characters. But this attitude is incorrect when it implies an *a priori* judgment of regarding *all* ethological characters as inferior to morphological ones as distinctive criteria. This assumption postulates the universal instability of the genetic mechanism governing ethological characters, which leads to admitting the existence of two different categories of genetic mechanisms, one, ruling morphological expression, being more stable than the other. Indubitably there are many ethological expressions

* Here the ethospecies concept is interpreted typologically, not categorically, as including not only the species distinguished only by ethological characters, but also those distinguished *mainly* by ethological characters. The original definition by Emerson, "the species primarily distinguished by their instinctive behavior" could be interpreted in this sense.

which are not fixed genetically. It is even conceivable that the number of genetically fixed characters is larger among morphological than among ethological ones. But there is no criterion which categorically separates the relative stability of these two groups. Both are either fixed genetically or not. When fixed, both are expressed phenotypically through coactions between environmental factors and genetic mechanisms, one as the spatiotemporal distribution of protoplasm and its products, the other as the spatiotemporal pattern of the movements of efferent organs or their products (as in nests), ruled by corresponding neural mechanisms, the roles of which are genetically fixed. The classification of animals has been made principally by using morphological characters. This tendency may and must continue for future studies. But once their relative stability has been established, any particular ethological characters are as effective as morphological ones in distinguishing various taxa.

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